CONSTRUCTION AND PRESERVATION OF TWO MODERN CORALLINE ALGAL REEFS, ST. CROIX, CARIBBEAN

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ABSTRACT. The internal structures of two coralline algal reefs from St. Croix are described. The primary framebuilders are *Lithophyllum congestum*, which dominates in exposed mid-intertidal situations, and *Porolithon pachydermum* from the high intertidal. Secondary frameworks are constructed by one of the following corallines: *Tenarea, Lithothamnium ruptile, Mesophyllum syntrophicum, Lithophyllum congestum*, and *Neogoniolithon* sp., together with *Homotrema* and vermetid gastropods. The environmental preferences of these corallines and their recognition in slabbed reef sections permits a reconstruction of past reef morphologies and environments. Predictable ecological successions are found within preserved coralline sequences which correspond with previous settlement plate experiments. The main agents of reef destruction are sponge and echinoid bioerosion. Inter-reef sediments are winnowed by wave currents and reflect the composition of surrounding coral reefs in addition to debris from the coralline algal reefs. A relatively low proportion of coralline algal debris in sediments around the reefs is thought to result from deposition of silt-sized sponge chips of corallines in quieter water elsewhere. Internal reef sediments reflect the composition of the reef constructors.

THIS work has arisen from research on Tertiary coralline limestones of the Tethyan region (Bosence and Pedley 1982; Bosence 1983*a, b*), during which it became evident that the interpretation of coralline limestones is limited by the paucity of studies on actuopalaeontology of Recent tropical coralline buildups. The longevity of coralline algal species together with their narrow environmental tolerances makes them valuable palaeoenvironmental indicators in the Tertiary (Adey *et al.* 1982; Bosence and Pedley 1982). Similarly, late Palaeozoic ancestral coralline reefs require descriptions of Recent counterparts for detailed interpretations.

It is here shown that there are two main components involved in reef construction. The major reef framework is constructed by primary framebuilders which support later encrustations by secondary framebuilders. The characteristics of present-day species of coralline can be recognized in thin sections from the slabbed reef material, and this permits reconstruction of the form and the ecological succession in ancient coralline reefs. Study of the modern reef sediments shows that those around the reef do not accurately reflect reef composition, but that those from the internal reef cavities are similar in composition to the reefs.

The St. Croix algal reefs (algal ridges) described here (text-fig. 1) were selected for investigation because of the extensive previous work on the present-day corallines by Walter H. Adey (Smithsonian Institution) and his co-workers. Adey (1975) describes the setting, morphology, large-scale internal features (text-figs. 2, 3), and Holocene development of the reefs. Adey and Vassar (1975) describe the colonization, succession, and growth rates of the corallines from a series of settling plate experiments. The environmental control on morphology of the main ridge-building alga *Lithophyllum congestum* is studied by Steneck and Adey (1976). The systematics and morphology of the corallines are to be described by Adey (pers. comm.). Detailed discussion of the relevance of these earlier studies to this project is included in the appropriate parts of this paper.

The ecology of the coralline algae (Adey 1975; Adey and Vassar 1975) provides the information for interpretation of the internal growth fabrics described below in this paper. In exposed situations in eastern St. Croix, a pavement of *Acropora palmata* exists in depths of 1–2 m. These coral pavements are coated by crusts of the coralline algae *Neogoniolithon* spp. and *Porolithon pachydermum*. If the
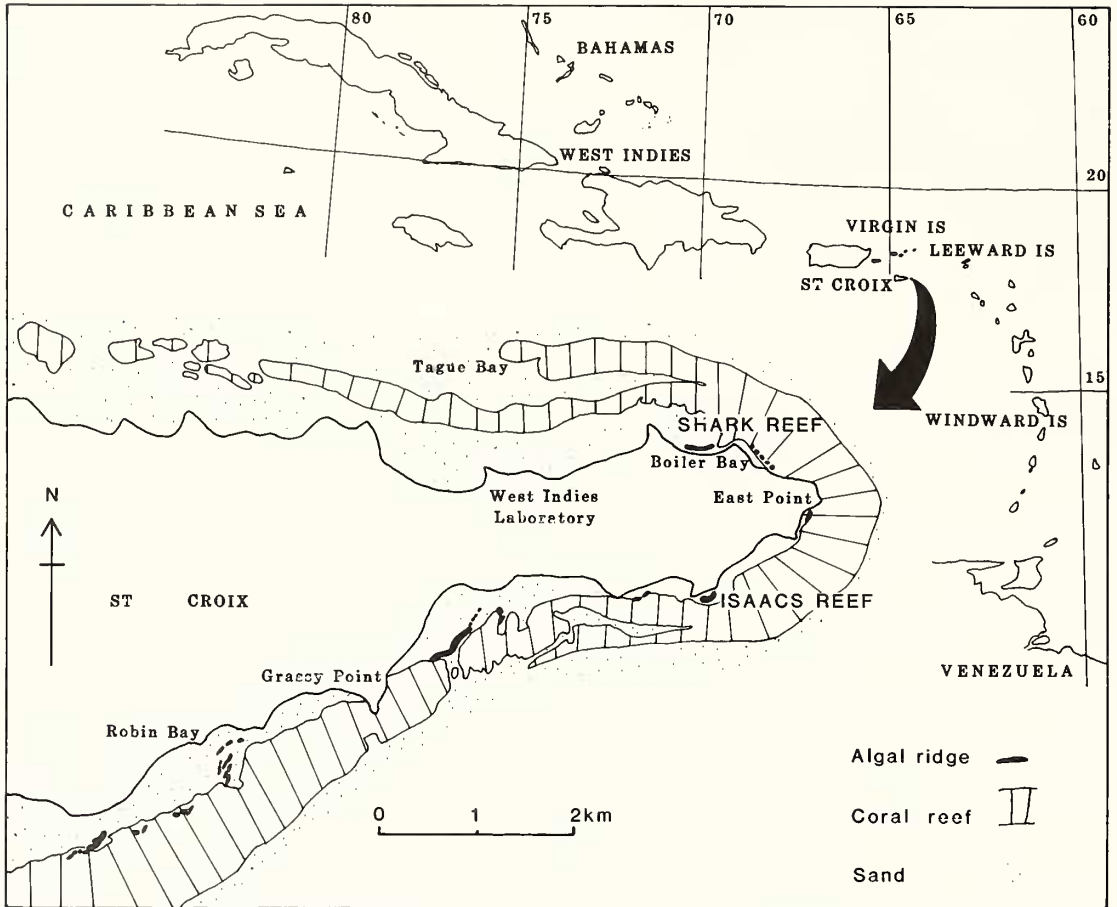
TEXT-FIG. 1. Location of Shark and Isaacs Reefs in St. Croix and the Caribbean (after Adey 1975).

pavements extend to low-water level then *L. congestum* dominates up to 20–30 cm above m.l.w.s. tides. Above this height *P. pachydermum* is the major reef constructor. In the many reef cavities and overhangs the following corallines are important in reef building: *Lithothamnium ruptile*, *Mesophyllum syntrophicum*, *Neogoniolithon* sp., and *Tenarea*. In addition, the foraminifer *Homotrema* and vermetid gastropods are common.

Two coralline ridges or algal reefs were selected for this study on the basis of those drilled by Adey (1975). Isaacs Reef is located off the exposed south-eastern shore of St. Croix (text-figs. 1, 2, 4B) and is composed of a number of fused reefs or boilers. The reefs are very cavernous with a number of walls and pillars supporting a roof and crest. Present-day coralline growth is luxuriant (text-fig. 4D, E) and construction by *Lithophyllum congestum* and *P. pachydermum* has built the reef to a height of up to 50 cm above m.l.w.s. tides (Adey 1975). Adey and Vassar (1975) give a maximum accretion rate of 5 mm/year for reef crest environments of exposed ridges. Adey's (1975) drilling indicates coralline build-up over a previous *A. palmata* reef dated at the base as 4,040 yrs. B.P. The *Acropora* continues today in 3–4 m of water in front of the algal reefs. Coralline frameworks extending to a depth of 2·5 m were recovered. For the present study a large slot 1 m deep and extending back 1·5 m from the reef crest was excavated to provide a continuous cross-section (text-figs. 2, 5).
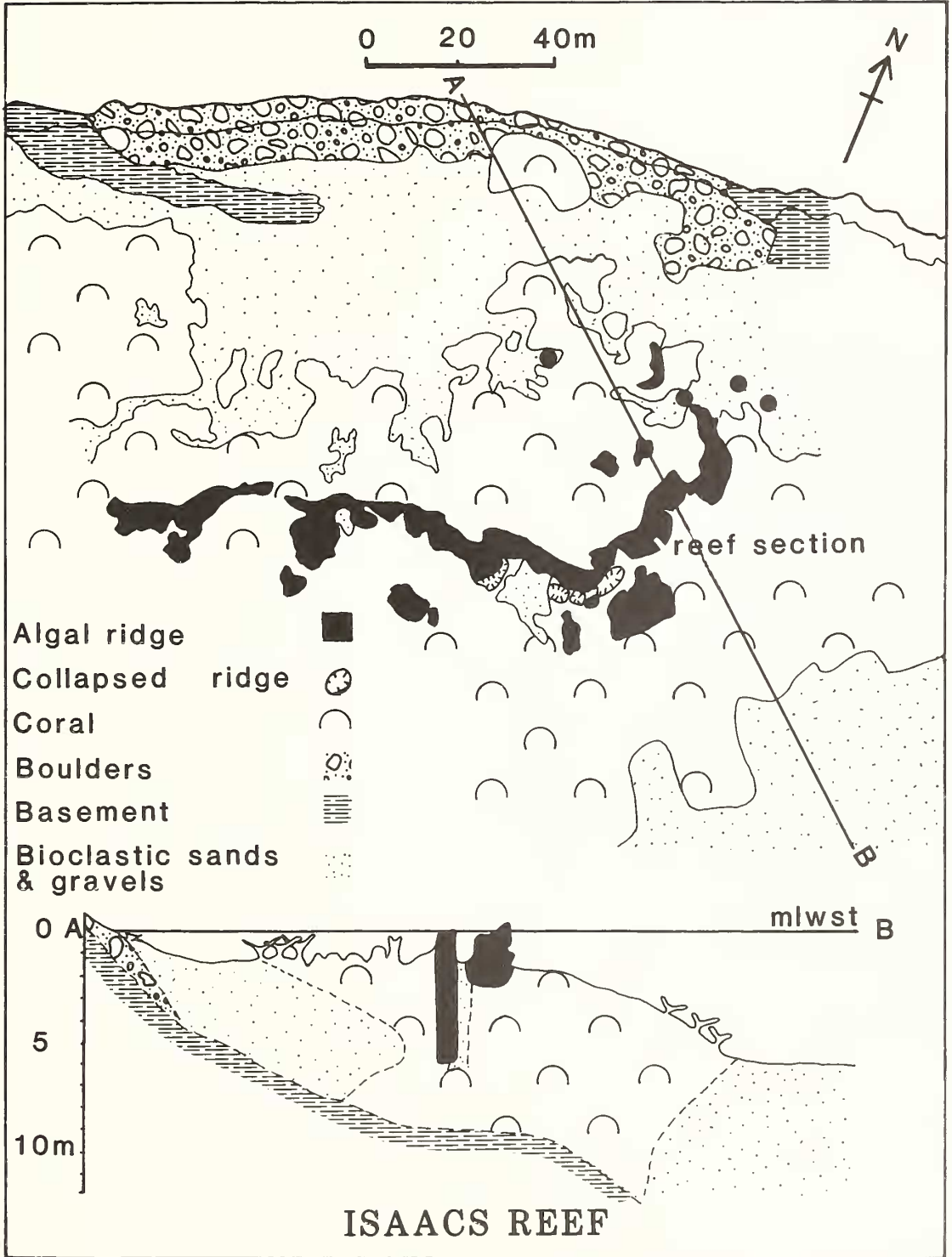
TEXT-FIG. 2. Plan and cross-section of Isaacs Reef showing location of algal reefs and excavated reef section (after Adey 1975). ● sediment samples.

Shark Reef, in contrast, occurs in the more sheltered Boiler Bay of north-eastern St. Croix (text-figs. 1, 3, 4A). It is further protected by a newly (*c.* 500 yrs. B.P.) emergent barrier reef extending across the bay (Adey 1975). Shark Reef was one of the most thoroughly studied of Adey's reefs (Adey 1975, figs. 39, 40). A large *A. palmata* stand (dated at 2,900 yrs. B.P.) is overgrown by about 1·5 m of coralline reef which extends today to a height of about 15 cm above m.l.w.s. tides. Because of the
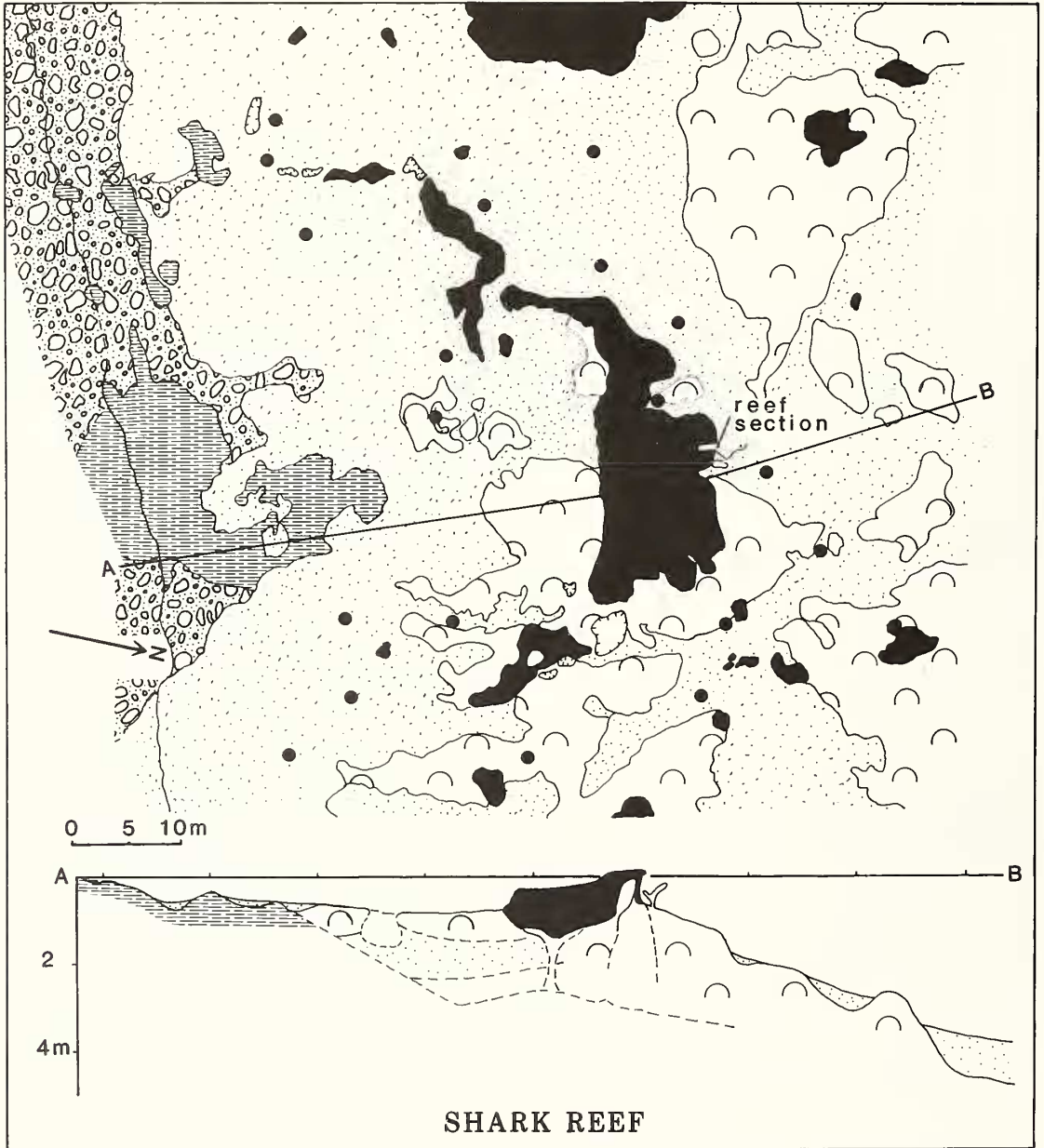
TEXT-FIG. 3. Plan and cross-section of Shark Reef showing location of algal reef and excavated reef section; symbols as for text-fig. 2 (after Adey 1975).

reduced hydraulic energy conditions there is little *Lithophyllum* and *Porolithon* growth on Shark Reef today (text-fig. 4c) although these algae are important in reef sections (text-fig. 6). Present-day surfaces are covered with non-calcified algae (Abbott *et al.* 1974) and penetrated by large borings of the echinoid *Echinometra*. Adey and Vassar (1975) have shown present-day accretion rates on these reef crests to be only 1–2 mm/year which apparently cannot keep pace with the heavy *Echinometra* boring (Adey 1975). As with Isaacs Reef a large slot normal to the reef crest was excavated (1·4 m deep and 1·2 m back from the crest), adjacent to and extending a previous slot of Adey (1975, fig. 40).

The depth/age relationships for these two reefs (Adey 1975) indicate an age of 2,200 yrs. B.P. for the base of my Isaacs Reef section and 3,300 yrs. for the base of my Shark Reef section. The slabbed reef sections (text-figs. 5, 6; Table 1) indicate five major components within the reefs. Primary reef frameworks are constructed by *L. congestum* and *Porolithon*. Secondary reef frameworks comprise

TEXT-FIG. 4. A, Shark Reef (arrowed); Boiler Bay, looking north-east. Note waves breaking on barrier reef across mouth of bay and small waves on beach. B, Isaacs Reef, looking south-west. Coralline algal ridges are clearly visible between waves. C, underwater photograph of Shark Reef crest, showing sparse crustose algal growth, white areas scraped by parrot-fish, and *Echinometra* in borings; × 0·12. D, surface view of Isaacs Reef crest, showing branching heads of *Lithophyllum congestum* and columnar growths of *Porolithon pachydermum* (upper centre, white). Darker tufts are fleshy algae (right of hammer). *Echinometra* borings (2–5 cm diam.) occur throughout the area; × 0·12. E, underwater photograph of front wall of Isaacs Reef (c. 1 m depth), illustrating competitive intergrowth of coralline crusts and vermetid (V) in secondary framework; note *Lithotrya* (L) borings; × 1.
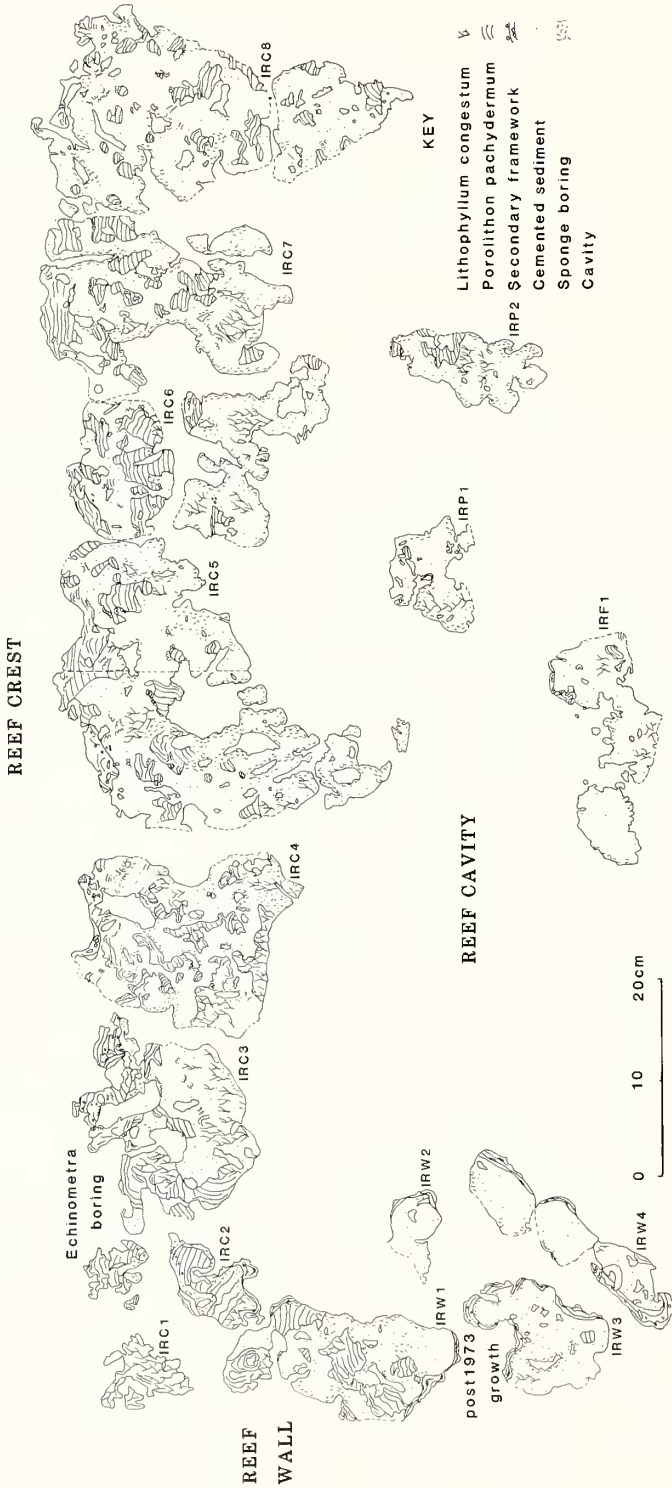
TEXT-FIG. 5. Section through Isaacs Reef crest, simplified from tracings of impregnated, cut, and polished reef blocks. Reef block labels refer to crest (IRC), wall (IRW), pillar (IRP), and floor (IRF) locations.

TABLE 1. Point counts from grid on slabbed reef surfaces (text-figs. 5, 6) indicating percentage abundance of frameworks, borers, sediment, and cavities ('Total' column includes counts from slabs and cavities; 'Preserved' column is recalculated for the preserved slabs only).

	Isaacs Reef (1378 counts)		Shark Reef (2272 counts)	
	Total	Preserved	Total	Preserved
Primary Frameworks	15	41	10	29
Lithophyllum congestum	5	14	2	7
Porolithon	10	27	5	14
Millepora	—	—	3	8
Secondary Frameworks	1	2	8	20
Tenarea–Homotrema	—	—	4	10
Sponge chambers	3	9	5	14
Cemented sediment	20	55	14	37
Cavities	61		62	

later crusts growing on and within the reef. Borings of sponges and other organisms account for 3% and 5% of Isaacs and Shark Reefs, respectively. Fourthly, cemented internal sediment forms a large part of the sections. Finally, reef cavities account for the majority of the cross-sectional areas (61% and 62% of Isaacs and Shark Reefs, respectively).

METHODS

The material for this study was collected during January 1980. Large blocks of reef were removed by hammer, chisel, and bar to excavate cuttings normal to the reef crest. Work on Shark Reef was straightforward because of low energy conditions but Isaacs Reef was continuously pounded by 1·0 to 1·5 m waves and ropes were used to maintain a position on the reefs. The reassembled blocks were slabbed along one plane, impregnated with Araldite resin, ground, and polished. Text-figs. 5 and 6 were traced from these prepared surfaces. Thin sections were prepared from further impregnated chips of both reefs for identification of the corallines, successional data, and study of the internal fabrics and sediments. Specimens of reef material were fractured, or polished, and etched, coated with gold for investigation under a JEOL JM 35 S.E.M. operating at 25 kv. Inter-reef sediments were collected with a scoop and sieved at half phi intervals. For all samples, subsamples from each sieve were amalgamated and impregnated. Composition was determined by point counts made on stained acetate peels.

THE CORALLINE ALGAE

An important part of this investigation involved the identification of the recently preserved coralline algae. The identifications were based on Adey's representative collection of coralline thin sections together with the original descriptions from decalcified material. Measurements from micrographs provided data on crust thickness, hypothallus thickness, hypothallus and perithallus cell sizes and shapes, heterocyst and conceptacle size and shape for the eight species of coralline from the Cruzan reefs (Table 2). Six of these species were found to be common or abundant on the reefs: *Lithothamnium ruptile* Foslie, *Mesophyllum syntrophicum* (Foslie) Adey comb. nov., *Lithophyllum congestum* (Foslie) Foslie, *Porolithon pachydermum* Foslie, *Neogoniolithon megacarpum* n.s. Adey,

and *Tenarea* sp. The remainder were rare: *Porolithon antillarium* Foslie and *Neogoniolithon imbricatum* n.s. Adey.

One other common coralline in the reef sections is represented by thin monostromatic crusts with roughly cubic cells (c. 10×12 μm). These occur as early colonizers of hard substrates in the reefs (see discussion below on ecological succession). They possibly correspond to Adey's genus *Leptoporolithon* which is a common early colonizer on these reefs. *Leptoporolithon* occurs as thin
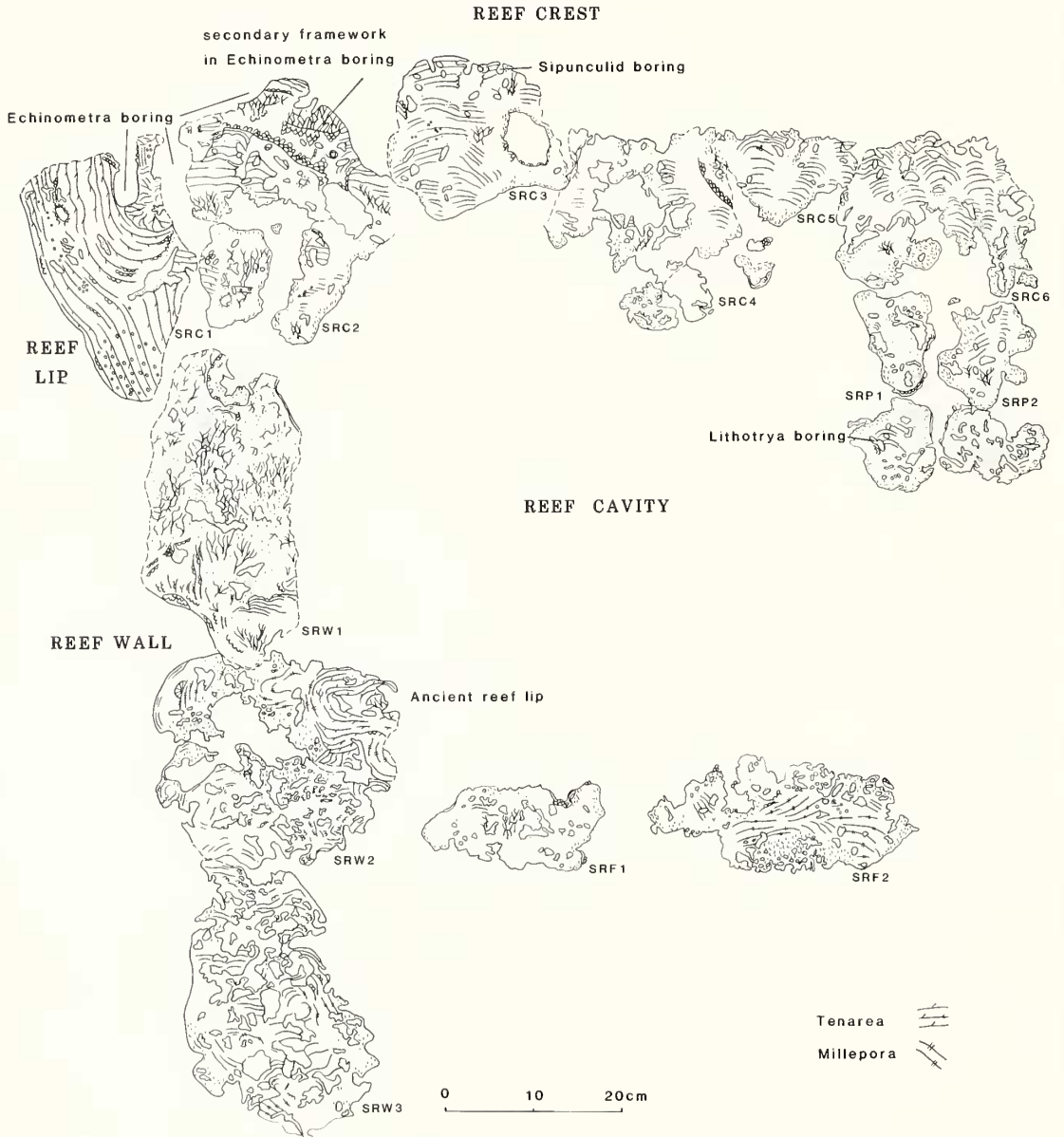
TEXT-FIG. 6. Section through Shark Reef crest, simplified from tracings of impregnated, cut, and polished reef blocks. Reef block labels refer to crest (SRC), wall (SRW), pillar (SRP), and floor (SRF) locations.

TABLE 2. Morphology of coralline algae. Measurement of each feature in microns expressed as mean (standard deviation), and range.

Taxon	Growth form	Hypothallus	Cell sizes	Perithallus	Cell sizes	Tetrasporic asexual conceptacles	Size width × height
Lithothamnium ruptile	Crusts of variable thickness	Non-coaxial 147 (4·5) 144–153 thick	29 (2·8) 25–34 × 11 (0·9) 10–13	Filaments dominant	29 (4·8) 25–36 × 12 (2·3) 8–15	Multipored	500–700 diameter
Mesophyllum syntrophicum	Folicaceous crusts	Coaxial 90 (12) 68–102 thick	24 (3·9) 19–32 × 7 (2) 5–10	Rows dominant	13 (3·6) 10–19·5 × 13 (6·2) 7–22	Multipored flat roofed	400–600 diameter
Lithophyllum congestum	Thick crusts and luxuriant branching in intertidal	Single layer sub-triangular or coaxial	13·5, 1–18·5 × 16, 5·5–24	Rows dominant branches zoned	5·5–11·5 × 7–8	Unipored	256 (60) × 106 (27)
Porolithon antillarum	Crusts and columns	—	—	Grid like, irregularly zoned Heterocysts in rows of 6–10	14 (2·4) 11–17 × 10 (2·1) 7–15 29·5 (4·8) 24–39 × 16 (3·3) 9–20	Unipored	253 (39) 235–272 × 111 (4·8) 105–117
Porolithon pachydermum	Crusts and columns	Coaxial	20 (2·2) 17–24 × 7 (1·4) 5–9	Filaments dominant regular grid Heterocysts in rows of 3–4	10 (3·7) 6–19 × 9 (1·7) 6–13	Unipored	101–185 68–88
Neogoniolithon megacarpum	Crusts c. 230 thick	Coaxial c. 50 thick	15 (1·7) 11·5– 17 × 5 (0·8) 3–7	Zoned irregular grid Heterocysts in filaments of 3–4	28 (11) 19–48 × 18 (2·5) 17–22 5 (1·2) 3–6 × 4·5(·7) 3–6 7 (3) 3–10 × 10 (1·6) 8–12	Large raised unipored	326 × 161
Neogoniolithon imbricatum	Thick crusts imbricate by overgrowing	Coaxial 88–92	22 (4·2) 17–29 × 9 (1·2) 8–12	Filaments dominant Heterocysts in filaments of 2–3	13 (4) 7–19·5 × 7 (1·8) 5–11 14 (3·6) 10–19·5 × 13 (3·3) 10–15	Unipored	500–1000 outside diam.

monostromatic crusts or developing a single-layered perithallus with heterocysts similar to *Porolithon* (Adey and Vassar 1975). No perithallus or conceptacles are present in the preserved monostromatic crusts. Because of the uncertainty over identification of these thalli they are here labelled 'monostromatic crusts'.

Full morphological details of each coralline are to be treated by Adey (pers. comm.). The diagnostic features of each species as seen in thin sections are tabulated in Table 2 and illustrated where relevant in Plates 50–52.

REEF CONSTRUCTORS

Primary frameworks

Lithophyllum congestum framework. Branching *L. congestum* may be abundant about 20 cm below to about 20 cm above m.l.w.s. tides in exposed ridges. The most exposed and therefore the highest ridges have the greatest cover of *L. congestum* (Adey 1975; Steneck and Adey 1976).

Of the two ridges investigated in the present study only Isaacs Reef supports live branching *L. congestum* (text-fig. 4D). This occurs as a 60 cm thick band on the outer crest of the reef. The lower part of this band has up to 2 cm thick crusts bearing incipient branches of *L. congestum* overgrowing old bored, infilled, and cemented reef (text-fig. 5, slab IRW1; Pl. 51, fig. 6). This represents new growth over a small slot cut by Adey in 1973 and gives an actual vertical crust accretion rate for crusts of 1 mm/yr. The branching *Lithophyllum* framework occurs as 5·3% of the area of the section (but 14% of the area of preserved reef—see table 1). The framework is preserved within the crest and the lower parts of the reef crest blocks (text-fig. 5, slabs IRC3–IRC7). Scattered areas are also preserved within the reef pillars and reef cavity floor (slabs IRP1–IRP2, IRF1). In contrast, Shark Reef, which has a similar porosity of just over 60%, has large areas of well-preserved branching framework in the front wall (text-fig. 6, SRW1; Pl. 50, fig. 3) but only small patches in other interior regions. The percentage area occupied by the framework is 2·5% or 14% of the preserved reef (area of slabbed surface).

L. congestum is preserved as an *in situ* irregular branching framework with or without a crustose base. Many areas are clearly remnants of previously more extensive frameworks because the margins are bioeroded (Pl. 50, fig. 1) and replaced by a secondary framework (Pl. 50, fig. 5) or cemented sediment. In addition to the areas of framework traced from the slabs, most thin sections contain small erosional relics of branching or crustose *L. congestum*.

EXPLANATION OF PLATE 50

Fig. 1. Polished slab (upper part of IRC6, text-fig. 5) illustrating preserved columnar growth of *Porolithon pachydermum* succeeding *Lithophyllum congestum* (lower right). Note well-cemented internal sediment (grey) within centimetres of upper growth surface of reef, × 0·5.

Fig. 2. Bases of articulate corallines (*Amphiroa*) in laminar crust of *P. pachydermum*. Note horizontal rows of heterocysts (arrow) within perithallial tissue. Thin section micrograph from block SRC3 (text-fig. 6), × 26.

Fig. 3. Section of lower lip of Shark Reef crest (SRC1, text-fig. 6). Branching *L. congestum* framework (upper right) is firstly overgrown by thick secondary framework of *Mesophyllum–Tenarea–Homotrema*-vermetid association then *Tenarea–Homotrema*-vermetid association. *Echinometra* boring (upper right) has geopetal infill of uncemented sediment, × 0·3.

Fig. 4. Thin-section micrograph showing detail of *Tenarea–Homotrema* framework with *Homotrema* (bottom centre) overgrown by successive crusts of *Tenarea*. Block SRW2 (text-fig. 6), × 10. Top to right of specimen.

Fig. 5. Vertical slabbed section from front wall of Shark Reef (SRW1, text-fig. 6) illustrating well-preserved *L. congestum* branching framework, small area of *Porolithon* framework (lower right) and *Echinometra* borings partly infilled with secondary framework (top centre). Secondary framework overgrows primary framework in lower left. Grey areas are hard cemented internal sediment, × 0·25.

Fig. 6. Thin-section micrograph of *L. congestum* framework illustrating branch fusion. Where filaments from adjacent branches meet end on (centre) a gap remains. Isaacs Reef crest (Block IRC1), × 10.

PLATE 50

BOSENCE, Coralline algal reefs

The initial colonization of *L. congestum* is in the form of crusts (Pl. 51, fig. 6). In lower reef wall positions, a laminar secondary framework of superimposed crusts may develop (e.g. slab IRCW1, text-fig. 5). The crusts may have grown in competition with *Homotrema* and/or *Tenarea* and this results in alternating layers of these organisms and *L. congestum* in vertical section (Pl. 51, fig. 6; text-fig. 8Dii). Similarly, crusts of *Lithophyllum* may be found within laminar and columnar growths of *Porolithon* (text-fig. 7). Branches arise from crust perithallial tissue to form branching frameworks (Pl. 50, fig. 5). Steneck and Adey (1976) give details of branch morphology which varies in different reef niches. Branch sections are frequently oval with minimum diameters of 1 mm and maximum diameters of 23 mm with a mean of 9·1 mm. Branches are constructed by a dominant central, zoned medullary hypothallus with elongate rectangular cells arranged in a grid of filaments and cell rows. The outer cortex of the branch is thin, with smaller square cells (Pl. 51, fig. 1). Branches may divide by apical or lateral division, but commonly fuse together (Pl. 50, figs. 5, 6) which increases the strength of the framework. Branch fusion occurs when filaments approach obliquely or laterally. However, when filaments from adjacent branches approach end on there is no fusion (Pl. 50, fig. 6) possibly due to a thick apical cuticle (cf. Cabioch 1972).

This framework is encrusted by *Homotrema*, vermetids, *Tenarea* sp. and monostromatic crustose corallines (Pl. 51, fig. 1) which all add to the branching framework. Less common encrusters are serpulids and bryozoans. Sediment, which is soon cemented, is added to the cavities between branches (Pl. 50, fig. 5) and is presumably brought in by waves.

Many outer surfaces are bored by dendritic algal borings (c. 10 μm diameter) which may also mark growth discontinuities within branches (Pl. 52, fig. 1). Surrounding the borings are darkened areas of altered algal tissue which under the S.E.M. are seen to be cells infilled with micrite cement. This close association suggests that micritization of the thallus may be controlled by the algae or organic decay in and around borings (cf. Bathurst 1971, p. 388). Sponge boring is ubiquitous and may occur before or after colonization by the encrusters mentioned above.

Porolithon framework. Three species of *Porolithon* occur in the St. Croix reefs: *P. antillarium*, *P. fragilis*, and *P. pachydernum* (Adey and Vassar 1975). The latter species is the main reef builder and dominates in high reef crest environments (over 20 cm above m.l.w.s. tides). Here it outcompetes *L. congestum* as *Porolithon* is particularly well adapted to resist desiccation and high levels of illumination (Steneck and Adey 1976; Littler 1973). On Isaacs Reef *P. pachydernum* is common both live on the upper reef crest (text-fig. 4D) and as a dense framework throughout the reef interior where it forms 10% of area in cross-section (text-fig. 5). The abundance decreases with depth into the reef as bioerosion increases and cemented sediment becomes dominant. In Shark Reef *Porolithon* is not


Fig. 1. Thin-section micrograph showing elongate zoned medullary cells and smaller, squarer cortical cells in outer part of branch of *Lithophyllum congestum*. Encrusting on coralline branches are *Homotrema rubrum* intergrown with monostromatic coralline crusts (arrowed). Isaacs Reef crest (IRC1), ×27.

Fig. 2. Thin-section micrograph showing detail of lacy intergrowth of *Lithothamnium ruptile* (note multipored conceptacle, mid left) and *Homotrema*. Block IRC3 (text-fig. 5), ×35.

Fig. 3. Thin-section micrograph of part of *Lithothamnium* (L)–*Tenarea*–*Homotrema* (H)–vermetid framework. Note early colonizers *Homotrema* and monostromatic crusts (M) on cemented internal sediment (lower right) giving way to *Lithothamnium* and *Homotrema* crusts (cf. text-fig. 8 Diii). Block IRW3 (text-fig. 5), ×24.

Fig. 4. *Mesophyllum* (M)–*Tenarea*–*Homotrema* vermetid (V) framework in Shark Reef Lip (SRC1; Pl. 50, fig. 3; text-fig. 6). Thin-section micrograph, ×10. Top to right of specimen.

Fig. 5. Thin-section micrograph of intergrowth of *Neogoniolithon* (N) and *Homotrema* (H) over earlier cemented sediment (upper right). Block SRW2 (text-fig. 6), ×10.

Fig. 6. Thin-section micrograph of laminar *Lithophyllum*–*Tenarea*–*Homotrema*-vermetid framework. Sponge-bored reef rock is overgrown in vertical sequence by *Homotrema* (H), Tenarea (T), *L. congestum* (L), vermetid gastropod (V) (infilled with aragonite cement), and *L. congestum*. Block IRW3 (text-fig. 5), ×25.

PLATE 51

BOSENCE, Coralline algal reefs
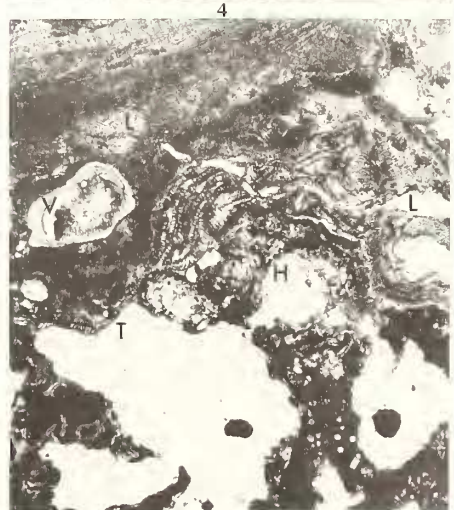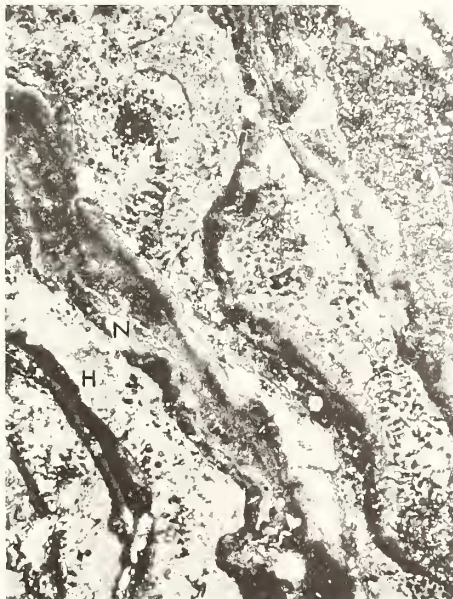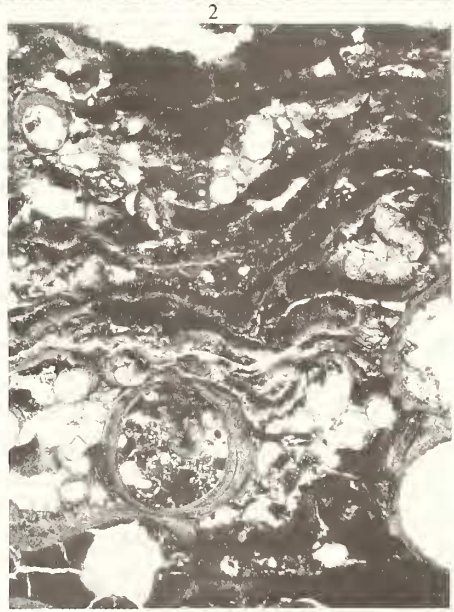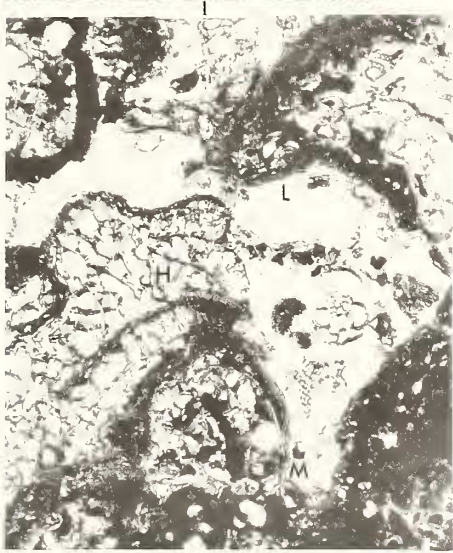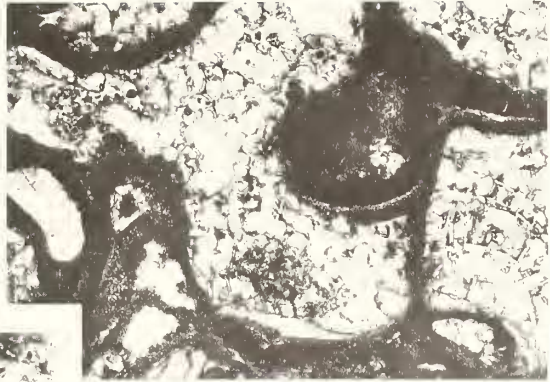
found living but it occurs in reef sections with a similar distribution to that found in Isaacs Reef. In the reef crest blocks it occurs as 8·4% of the area but *Porolithon* only makes up 4% of the reef floor blocks. *Porolithon* frameworks dominate over *Lithophyllum* frameworks in the inner crest regions whilst *Lithophyllum* dominates the outer crest and wall locations (cf. text-figs. 5, 6).

P. pachydermum occurs as thick crusts with a thin poorly developed hypothallus. The thick perithallus with cells arranged in filaments and with frequent heterocysts and conceptacles, is apparently of limitless growth. The perithallial tissue forms laminar crusts which normally develop into columnar growths (1·0–1·5 cm high and 1 cm wide) of undifferentiated tissue (Pl. 50, fig. 2). The growth of columns can be seen to have been discontinuous with breaks and rehealed surfaces being common. Algal borings (10 μm) persist throughout the columns suggesting continuous infestation of *Porolithon* during life (text-fig. 7). A common epiphyte is the articulate coralline *Amphiroa* (Pl. 50, fig. 2; text-fig. 7). Articulate corallines are not usually preserved *in situ* but here the bases have been overgrown by the live host to become incorporated in the *Porolithon* tissue.
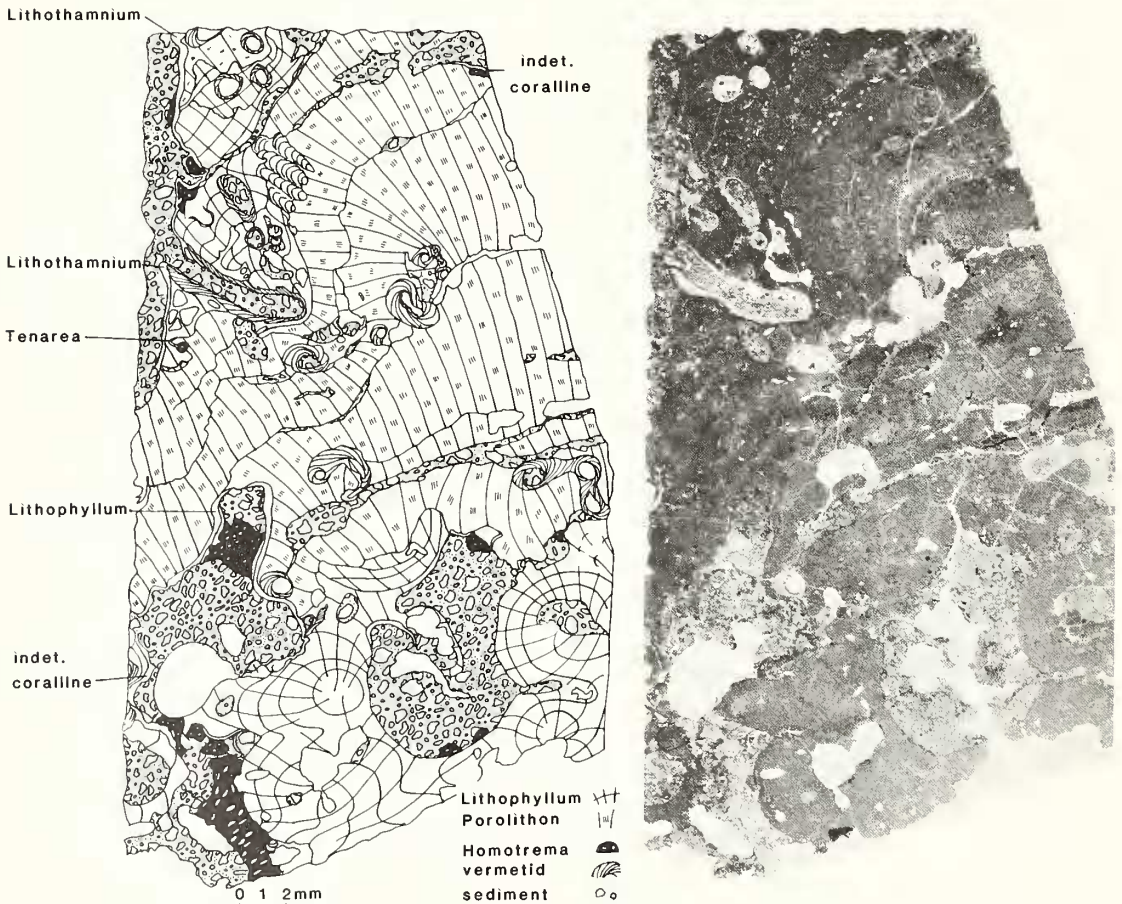
TEXT-FIG. 7. Thin-section micrograph and tracing to illustrate structure and succession in primary frameworks (branching to laminar *Lithophyllum congestum*, then columnar *Porolithon pachydermum* followed by *Lithophyllum* and *Porolithon* crusts), and secondary *Lithothamnium* and *Lithophyllum* crusts. Note frequent intergrowths of *Homotrema* and vermetid gastropods, infilled sponge borings, minor growth breaks and subvertical algal borings in *Porolithon*.

This relationship is not found in any other coralline in the St. Croix section and appears to be host specific. *Amphiroa* debris is common in the reef sediments. Vermetids and *Homotrema* are commonly intergrown within the *Porolithon* framework. Sponge boring is ubiquitous.

Secondary frameworks

Within the many reef cavities and below overhangs exist associations of encrusting corallines and other epizoans. The term secondary framework is used to describe these cryptic crustose associations because they overgrow or infill cavities in primary frameworks or cemented sediment and they make up a minor part of the two reef sections (0·7% and 7·7% of Isaacs and Shark Reef, respectively).

The major taxa involved in the construction of secondary frameworks as seen in thin section are: *Lithothamnium ruptile*, *Mesophyllum syntrophicum*, *Lithophyllum congestum* (crustose forms), *Neogoniolithon* sp., *Tenarea* sp., Vermetid gastropods, and Homotrematid foraminifers. Adey (1975) also lists *Archaeolithothamnium dimotum* as a cryptic coralline but this has not been seen in these sections.

TABLE 3. Frequency of pairing (total 77) of taxa in encrusting associations in thin section.

	Lithophyllum congestum	Lithothamnium ruptile	Neogoniolithon	Mesophyllum syntrophicum	vermetid	Homotrema
Tenarea	6	3	3	5	8	19
Homotrema	5	6	3	4	9	
vermetid	1	2	1	2		
Mesophyllum syntrophicum	0	0	0			
Neogoniolithon	0	0				
Lithothamnium ruptile	0					

Of the 7 encrusting taxa only some (15 pairs out of a possible 21 pairings) are found together in these frameworks. The crusts normally occur as alternating layers of 3 or 4 taxa in an association. Table 3 shows the frequency of occurrence of pairs (substrate and overgrowth) of encrusting organisms in secondary frameworks. The coralline *Tenarea* is abundant and ubiquitous (accounting for 63% of pairings) whilst *Homotrema* and vermetids are respectively less and less common but still ubiquitous. The corallines *Neogoniolithon* sp., *M. syntrophicum*, *L. congestum*, and *Lithothamnium ruptile* commonly overgrow or are overgrown by *Tenarea*, *Homotrema*, and vermetids but do not occur together in secondary crustose frameworks. This pattern of association permits a classification into five principal secondary frameworks in which *Tenarea*, *Homotrema*, and vermetids may occur alone or together with one of four other diagnostic coralline taxa, *viz.*

Tenarea–Homotrema–vermetid framework;
Lithothamnium–Tenarea–Homotrema–vermetid framework;
Mesophyllum–Tenarea–Homotrema–vermetid framework;
Neogoniolithon–Tenarea–Homotrema–vermetid framework;
Lithophyllum–Tenarea–Homotrema–vermetid framework.

All these frameworks are constructed by laminar to foliaceous crusts of corallines intergrown with *Homotrema* and vermetids. The competitive intergrowth of these corallines can be seen today in close up underwater photographs (text-fig. 4E) from overhangs and reef cavities. In vertical thin sections an interfingering growth of adjacent encrusters indicates competitive growth (Pl. 51, figs. 2–6). Cavities within these frameworks may be common where thin, foliaceous crustose growth occurs (*Lithothamnium–Tenarea–Homotrema*–vermetid framework) or rare where thick laminar crusts are

involved (*Neogoniolithon–Tenarea–Homotrema*-vermetid framework). Similarly, bioerosion is commoner in the latter, denser frameworks than in the former, more open frameworks. Cavities are either open, infilled with sediment, or filled with fans of aragonite cement (Pl. 51, fig. 6).

The secondary frameworks listed above are found in different environments on and within the reefs. The *Tenarea* dominated framework (Pl. 50, figs. 3, 4) is commonest on the underside of Shark Reef crest (SRC1, text-fig. 6; Pl. 50, fig. 3) and in what is interpreted as a fossil reef crest on block SRW2 (text-fig. 6). In both situations it overgrows a branching head of *Lithophyllum congestum*. Occasional thin crusts of this association (but with *Homotrema* dominating) are found over growth breaks in the primary frameworks.

The *Lithothamnium–Tenarea–Homotrema*-vermetid framework is found in both reef sections in similar successional positions. Most occurrences follow erosion or overgrow fresh *Lithophyllum congestum* or *P. pachydermum* frameworks. Other occurrences are where it alternates with the *Lithophyllum–Tenarea–Homotrema*-vermetid framework. Normally this association occurs in reef cavities (i.e. infilling *Echinometra* borings: SRC2, text-fig. 6). However, with sections deeper within the reef it is not possible to reconstruct the surrounding niche due to later boring and reef growth.

The *Neogoniolithon*-dominated association is found in the lower reef front wall of Shark Reef (SRW 2, text-fig. 6) and the *Mesophyllum*-dominated association occurs in cryptic habitats on both reefs (Pl. 50, fig. 3; Pl. 51, fig. 3). This association occurs with the large *Tenarea–Homotrema*-vermetid framework on the underside of the Shark Reef crest. It is also found on blocks on the floor of reef cavities (text-fig. 5, IRF1; text-fig. 6, SRF1).

The main occurrence of the *Lithophyllum–Tenarea–Homotrema*-vermetid framework is in the recently exposed areas on Isaacs Reef crest (text-fig. 5, IRW2–IRW4; Pl. 51, fig. 6). This occurrence represents the first stage in the development of the *L. congestum* branching framework and has been described above.

Discussion

The occurrence of coralline frameworks in the reefs is shown above to be closely tied to the specialized ecological requirements of the different coralline algae. Therefore, the presence of preserved frameworks in the reef sections (text-figs. 5, 6) can be used to reconstruct ancient reef morphology and environments. In both reef sections there is no evidence of any major erosion surfaces or breaks in growth. Therefore, reef growth is considered to be more or less continuous.

Isaacs Reef. The presence of preserved remnants of branching *Lithophyllum* and *Porolithon* frameworks in the interior of blocks at the bottom of the Isaacs Reef section (IRF1, text-fig. 5) indicate the former (*c*. 2,200 B.P.) presence of a high-intertidal reef forming in high energy conditions. Nothing is preserved of the shape or position of the reef crest. The base of the present-day ridge crest blocks (particularly IRC3, 4, 6, 7, text-fig. 5) records the change from an exposed mid-intertidal *Lithophyllum* reef to a high-intertidal *Porolithon* reef. The downward-curving *Porolithon* growth laminae in block IRC3 suggest a former outer edge to this reef crest. A high intertidal *Porolithin* reef crest has continued through to the present day with *Lithophyllum* on the front of the seaward edge.

Shark Reef. Extensive drilling by Adey (1975) showed that Shark Reef was founded on heads of *Acropora palmata* and *Millepora*. The present section penetrates to the top of the *Millepora* colonies. Overgrowing the *Millepora* are alternating frameworks of *Lithophyllum* and *Porolithon* (blocks SRF1, 2, text-fig. 6). The inner part of block SRW2 (text-fig. 6) shows a branching *Lithophyllum* framework overgrown by 2–6 cm thick convex-outwards secondary frameworks of both *Tenarea* and *Mesophyllum–Tenarea–Homotrema*-vermetid type. These frameworks are only found together today on the outer crest and lip of the sheltered Shark Reef (block SRC1, text-fig. 6). Therefore, this structure may be interpreted as an ancient reef lip developing as a response to quieter hydraulic conditions. This sheltered reef crest is succeeded within a few centimetres by *Lithophyllum* then *Porolithon* and then nearly 50 cm of well-preserved branching *L. congestum*. This represents a return to an exposed intertidal reef crest, (bock SRW1, text-fig. 6). The remaining 30 cm of reef crest blocks record a high intertidal *Porolithon* crest with occasional intergrowths of branching *Lithophyllum*. The upper reef surface today is not concordant with this growth framework. Extensive *Echinometra*,

sipunculid, *Lithotrya*, and algal borings are eroding this surface and no live *Porolithon* has been recorded. These sheltered conditions are also recorded by the thick *Tenarea–Homotrema*-vermetid and *Mesophyllum–Tenarea–Homotrema*-vermetid secondary frameworks on the outer and under surface of the lip. Adey (1975) has suggested that the sheltered conditions are due to the build up of an *A. palmata* barrier reef across the mouth of Boiler Bay (text-fig. 4A) in the last 500 years.

ECOLOGICAL SUCCESSION

The change, through overgrowth, of one association of corallines to another is recorded in vertical sections in the reef slabs. Large-scale changes in frameworks have been discussed in the preceding sections. The reef frameworks in thin section illustrate ecological succession on a smaller scale. This is shown where fresh (broken) substrates are colonized or where new individuals overgrow and replace previous corallines. In this investigation, 350 overgrowths were recorded and the nature of the junction (bored, broken, simple) was observed. Overgrowths by the same species were not recorded. The successions were analysed by the probability of one taxon being overgrown by another. The sequences were studied within primary frameworks, overgrowths to primary frameworks, and secondary frameworks in the reef crests, walls, and interiors (text-fig. 8).

Succession within primary frameworks

In primary frameworks the commonest growth sequences, with or without a time break (which is indicated by boring into the substrate), is from laminar to branching *Lithophyllum* followed by an overgrowth of first laminar then columnar *Porolithon*. Columnar *Porolithin* is most commonly overgrown by *Lithophyllum* crusts (text-figs. 7, 8A). These observations confirm the large-scale association of these two frameworks and, because of the differing tolerances to exposure of these taxa, reflect fluctuating conditions of emergence. This could result from breakage of portions of reef in storms (there is evidence of this happening on the present-day reefs) or fluctuating sea level. Adey and Vassar (1975) measure accretion rates of 1–5 mm/yr which means that successions without a time break represent changes measured in years or tens of years. This short time span suggests that growth or breakage of reef crest sections is the most likely cause of local alteration of conditions of exposure.

Primary framework encrusters

The frequencies of overgrowths by encrusters on the primary reef frameworks are illustrated in text-fig. 8B and C. Breaks within *Porolithon* thalli are colonized mainly by *Tenarea* and *Homotrema* which are also the commonest encrusters on the preserved outer surfaces. None of the growth breaks within *Lithophyllum* was found to be colonized by other taxa. This may reflect the rapid growth rate of this coralline (up to 8 mm/yr, Steneck and Adey 1976). The commonest encrusters, mostly over dead bored branches of *Lithophyllum*, are *Homotrema*, *Tenarea*, and monostromatic crusts.

Secondary frameworks

An analysis of secondary frameworks identified five associations of encrusters. Within these associations there were alternations of overgrowth resulting in the accreting frameworks. This analysis records the sequence of overgrowths within these frameworks and between one association and another. Results of recording successions from the reef crests and interior cavities from both reefs were similar and have been combined for discussion (text-fig. 8D). Overgrowths in the Shark Reef wall were markedly different and are discussed separately (text-fig. 8E). Reef crest and wall and interior cavities are characterized by a large number of combinations (36 out of a possible 72 overgrowths) of a relatively small number of encrusters (8 corallines + *Homotrema*). Text-fig. 8D therefore only shows the commonest recorded sequences. Bored and broken surfaces and reef rock are most commonly overgrown by *Homotrema*, *Tenarea*, and monostromatic crusts (Pl. 51, figs. 3, 6).

The pattern of subsequent colonization is again dominated by associations of *Lithothamnium ruptile* or laminar *Lithophyllum* or *M. syntrophicum*, all with *Tenarea* and *Homotrema*. The

succession of one of these associations by another is only occasionally found and is most commonly an alternation of laminar *Lithophyllum* and *Lithothamnium* frameworks (text-fig. 8Dii, Diii).

The Shark Reef wall overgrowth sequences are shown in text-fig. 8E. They differ from the previous overgrowths by the addition of large colonies of *Millepora* and crusts of *Neogoniolithon* (Pl. 51, fig. 5) and *Porolithon*. *Lithophyllum* and *Mesophyllum* are lacking and *Lithothamnium* is less frequent.

Discussion

The present-day succession of corallines on the St. Croix reefs has been studied by Adey and Vassar (1975). Plates placed in well-lit areas in 1–2 m of water in Boiler Bay were studied over a year. At or before 20–60 days *Leptoporolithon* spp. dominate. *Tenarea* increases in importance up to 100 days and then *Neogoniolithon* increases at the expense of the early successional species. If grazing is heavy on plates *Leptoporolithon* and *Tenarea* may increase. In shady reef cavities *Tenarea*, *Lithothamnium ruptile*, *Hydrolithon borgesenii* occur. Adey and Vassar (1975) did not record the occurrence of *Homotrema*.
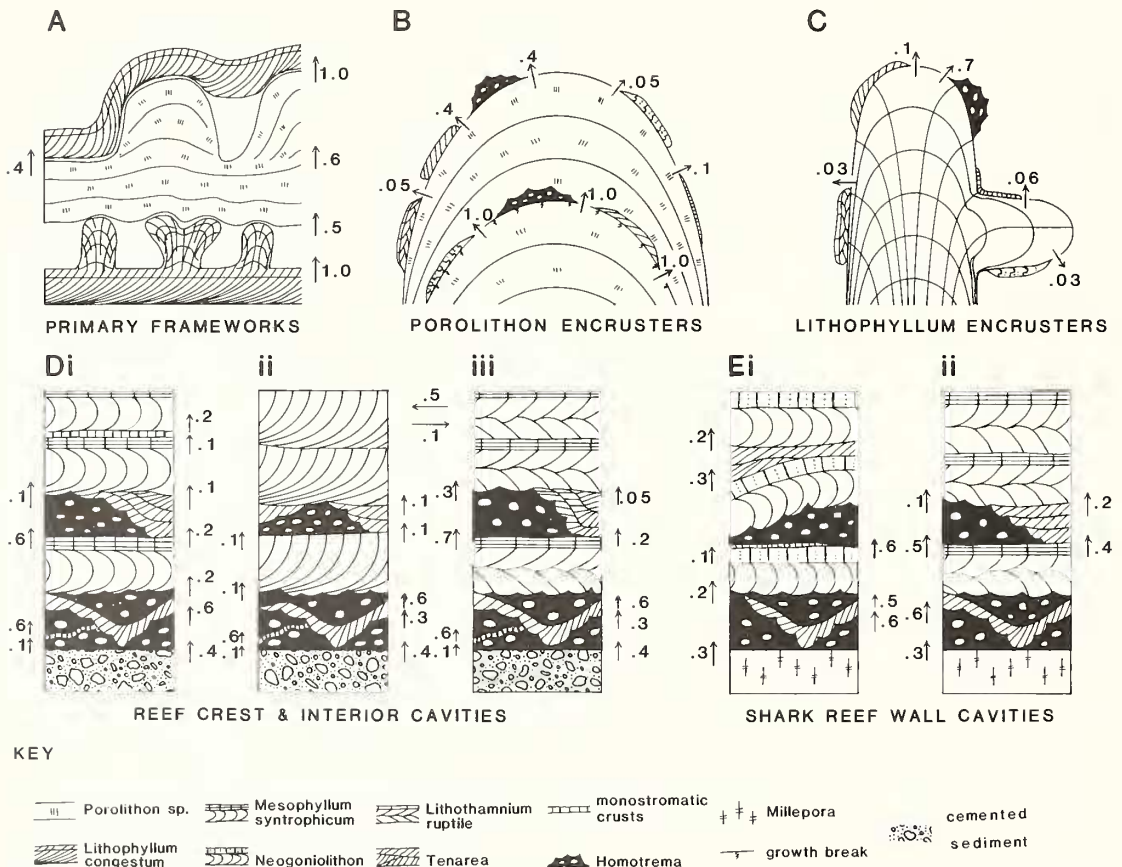
TEXT-FIG. 8. Ecological succession in coralline algal ridge frameworks. Arrows and numbers give direction and probability of the particular overgrowth illustrated; data from 352 observations of thin sections. A, succession of growth forms in *Lithophyllum* and *Porolithon* primary frameworks. B, frequency of encrusters within and on *Porolithon* frameworks. C, frequency of encrusters on *Lithophyllum* frameworks. Di–iii, succession within secondary frameworks in reef crests, interior cavities, and wall of Isaacs Reef. Ei, ii, succession in secondary frameworks within Shark Reef wall cavities.

A comparison of these successional patterns on plates with the vertical sequences described above (text-fig. 8) indicates many similarities, including the pioneer colonization by *Tenarea* and monostromatic crusts (*cf. Leptoporolithon*), and the later occurrence of *Lithothamnium ruptile* and *Tenarea* in cryptic environments. However, I additionally record later colonizations by *M. syntrophicum* and *Lithophyllum congestum* on both Isaacs and Shark reefs. *Neogoniolithon* occurs mainly in the reef wall of Shark Reef which corresponds to the positions of the settlement plates in Boiler Bay (Adey and Vassar 1975). Additional information here comes from the presence of *Lithothamnium ruptile* overgrowing fresh, branching *Lithophyllum congestum* in exposed areas. No *Lithophyllum* or *Porolithon* settled on the Boiler Bay plates but these appeared after 6 months on plates on the more exposed Fancy Algal ridge (Adey and Vassar 1975). The large degree of similarity between the results from these two investigations provides valuable evidence that ecological succession can be established with considerable accuracy from fossil material.

In a study of secondary frameworks from Recent and Pleistocene reefs in Barbados, Martindale (1976) noted no colonization succession in plates or vertical sections of crusts. However, Martindale (1976) does record a larger-scale successional change in fossil crusts over coral colonies. These represent the change from open, well-lit coralline associations (*Lithophyllum*, *Porolithon*, and *Neogoniolithon*) to cryptic associations of corallines (*Mesophyllum*, *Lithothamnium*, *Archaeolithothamnium*), bryozoans, serpulids, and foraminifers. He interprets these trends as recording the change with burial as the *Acroproa palmata* thickets build up.

In reviewing ecological succession, Connel and Slatyer (1977) propose three process models to explain succession: (1) a facilitation model where successional colonizers modify the environment and make it suitable for later species, (2) a tolerance model where first arrivals are fast growing, rapid dispersers and later animals are better able to utilize resources, and (3) an inhibition model where no replacements occur until damage creates an opening which is then occupied by longer lived genera. The St. Croix data does not fit the facilitation model as colonizers in each case are encrusting a coralline substrate. Similarly, the inhibition model is inappropriate as Adey and Vassar (1975) have shown that succession returns to the pioneers after disturbance by heavy grazing. The available data best fits the tolerance model, for which Connel and Slatyer could find little supportive field evidence. Later organisms which overgrow the pioneers, are larger, more robust and longer lived than the thin, early colonizing monostromatic crusts and *Tenarea*. Grimes (1977) also suggests that vegetational successions are characterized by the replacement of small rapid dispersers, which are efficient at acquiring new space, by larger more durable and massive forms.

BIOEROSION

In both reef sections, both primary and secondary frameworks are bored to a variable degree (text-figs. 5, 6; Pl. 52). The main characteristics of these borings are similar to those described from Caribbean (Scoffin *et al*. 1980) and Bermudan (Ginsburg and Schroeder 1973; Scoffin and Garrett 1974) patch reefs with the exception of bivalve borings.

Echinoidea

Borings made by *Echinometra lucunter* are common today on the upper surfaces of both reefs (text-figs. 5, 6; Pl. 50, figs. 1, 3, 5; see also Abbott *et al*. 1974). Juveniles occupy spaces between coralline branches and as they grow specimens can be seen to have enlarged their holes by removing adjacent corallines. Borings are commonly up to 3–4 cm in diameter but may occasionally reach 6 cm. They penetrate down from the reef crest and sideways into the front wall of the reefs (text-figs. 5, 6) with sinuous J and U shapes in vertical section. Margins of occupied borings are clean, sharp, and truncated frameworks or cemented reef sediments. Stomach contents of *Echinometra* from Shark Reef contain 5–10% carbonate material by volume which is composed almost entirely of coarse sand-sized fragments of articulate corallines. Very occasional fragments of *Homotrema*, vermetids, crustose corallines, and reef rock are also found. Abbott *et al*. (1974) found that *Echinometra* grazed indiscriminately on epiphytes in Boiler Bay and record a positive correlation between occurrence of

taxa in gut contents with abundance of epiphytes on reefs. Grazing traces are common on both reef surfaces. Secondary crustose frameworks occur in both present-day and ancient *Echinometra* borings (text-fig. 6, slab SRC2; Pl. 50, fig. 5). Margins of borings may also contain smaller borings of sponges and algae.

Diadema antillarium is also a common grazer on the under surfaces of Shark Reef. Possible *Diadema* faecal pellets (cf. Hunter 1977) are found in the coarse fractions of inter-reef sediments (see below).

Lithotrya

Straight, subvertical borings by this endolithic barnacle are common on both reef crests (Pl. 52, fig. 3). They possess a distinctive oval cross-section (maximum diameters 5 and 10 mm; see Ahr and Stanton 1973). Margins to borings are sharp, smooth, and cut through both coralline framework and cemented reef sediment. Sinuosity is only seen where borers have to make a deviation around previous cavities. Borings penetrate to a maximum depth of 10 cm.

Sipunculoidea

Sipunculid worm borings are common on the upper reef surfaces (text-fig. 6). They are characterized by smooth-walled, sinuous borings which are circular in cross-section (maximum diameter 9 mm), and reach lengths of 4 cm. The borings typically have a rounded blind end within the reef.

Clionidae

Chambers produced by clionid sponges are ubiquitous in reef slabs (text-figs. 5, 6; Pl. 52, figs. 2–4). Empty chambers account for 9 and 13·6% of the preserved blocks from Isaacs and Shark reefs, respectively. Both interior and exterior reef surfaces are bored, together with surfaces or previous larger borings. S.E.M. study reveals the characteristic sculpted surfaces of chambers and the excavated chips (Pl. 52, figs. 2–5). The chips form a significant proportion of the fine-grained intra-reef sediments (see below).

Algae

Endolithic algae are common as borers, particularly within coralline thalli. Their nature and occurrence is described above under *Lithophyllum congestum* and *Porolithon* primary frameworks.

EXPLANATION OF PLATE 52

Fig. 1. Thin-section micrograph illustrating bored growth break in *Lithophyllum congestum*. Isaacs Reef crest (IRC1), × 36.

Fig. 2. S.E.M. micrograph of clionid sponge boring with excavated (scalloped) chip and other skeletal debris. Block SRC5 (text-fig. 6), × 436.

Fig. 3. *Lithotrya* (L) borings in reef fragment from Isaacs Reef Crest. Note characteristic smooth oval cross-section. Outer margin of specimen well-bored by clionid sponge(s), × 1.

Fig. 4. S.E.M. micrograph illustrating clionid sponge-bored coralline infilled with micrite peloids and skeletal debris with later endolithic algae. Block IRC4 (text-fig. 5), × 458.

Fig. 5. S.E.M. micrograph of fresh clionid sponge boring in micritized coralline. Note characteristic pitted surface where chips have been removed. Block IRC4 (text-fig. 5), × 24.

Fig. 6. Thin-section micrograph of cemented internal sediment illustrating abundant micrite and spar-cementing peloids, grains of *Homotrema*, and articulate coralline (lower right). Block SRF1 (text-fig. 6), × 100.

PLATE 52
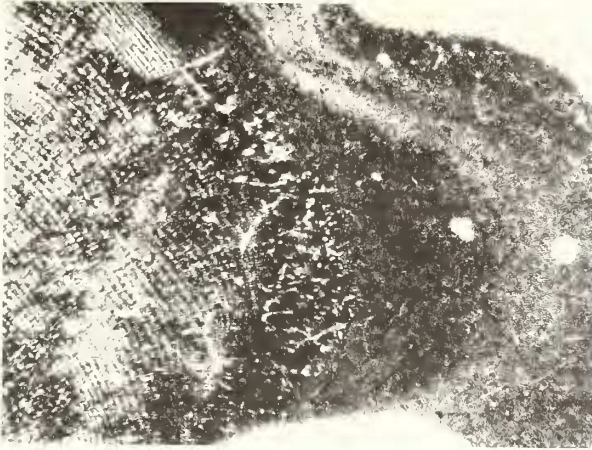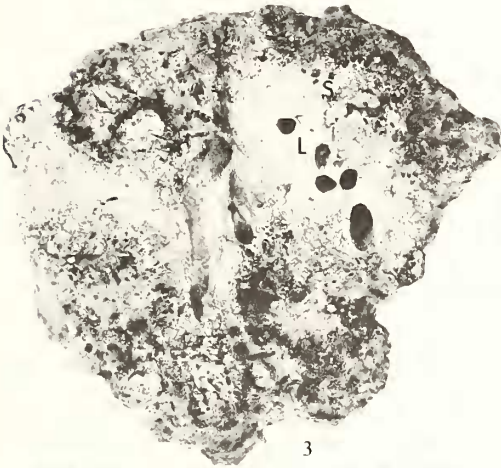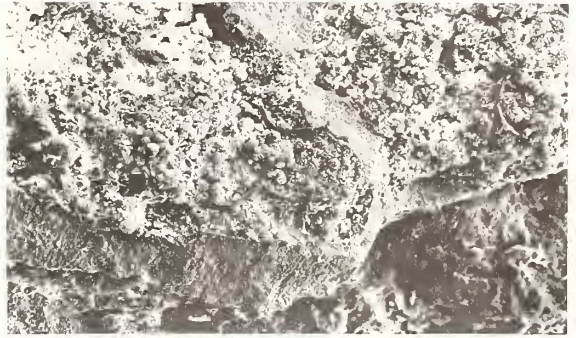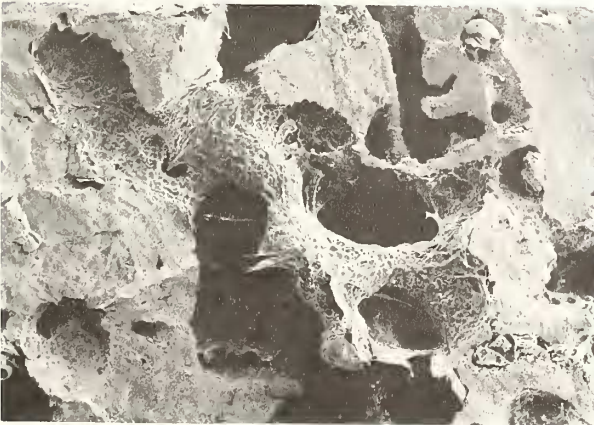

BOSENCE, Coralline algal reefs

REEF SEDIMENTS

Inter-reef sediments

The algal reefs are surrounded by coral and coralline algal pavements covered with patches of bioclastic sediment. The sediments are commonly wave-rippled during normal wave conditions and support sparse and patchy populations of *Penicillus*, *Halimeda*, and *Thalassia*. The size distribution and composition of these sediments is shown in text-fig. 9. The sediments from Isaacs Reef are very coarse sands which are moderately well to poorly sorted. They possess a near symmetric to coarsely skewed frequency distribution, the coarse tail being composed of a small number of large coral, mollusc, or coralline fragments. Constituent composition varies with grain size. Crustose corallines, foraminifers, and intraclasts (mainly cemented internal sediments from reefs) decrease, and corals increase in abundance with decreasing grain size. From a visual impression it appears that the sediment grain composition reflects the abundance of grain producers in the environment (see text-fig. 2), the only exception being *Halimeda* plates which appear over-represented in the sediments. Clionid sponge chips occur in the finest grades (S.E.M. examination) but the majority are probably too small to be deposited in these wave-swept sand patches.
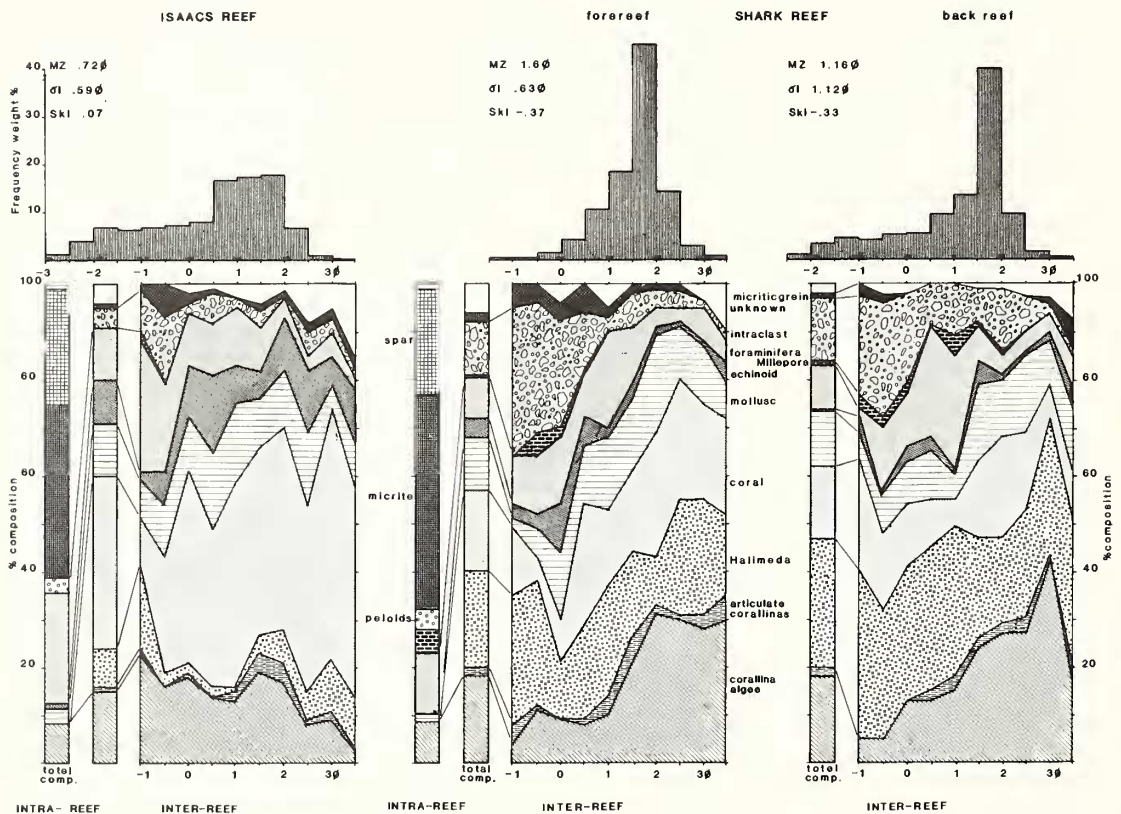
TEXT-FIG. 9. Texture and composition of sediments from Isaacs and Shark Reefs. Size-frequency histograms illustrate typical size distributions; point counts of inter-reef sediments were taken from peels of samples combined from each size class of all field samples; intra-reef sediments point-counted from six thin sections from each reef.

Shark Reef sediments have been divided into those from the fore and back reef areas for presentation (text-figs. 3, 9). Both areas have very coarse sand to granule-sized sediments which vary from very well to very poor sorting, the best-sorted sediments being in sand patches of the fore reef region which are being continually transported by wave currents. Small numbers of gravel-sized bioclastic grains result in grain size distributions that are coarsely to strongly skewed.

Sediment composition contrasts with that from Isaacs Reef in that *Halimeda* grains are about twice as abundant at the expense of coral grains. This is matched by an increase in cover of *Halimeda* around the patch reefs compared with Isaacs Reef. An almost pure *Halimeda* gravel forms the beach sediment behind the reefs. Also contrasting with Isaacs Reef, is an increase in abundance of coralline grains with decreasing grain size. Intraclasts, some of which resemble *Diadema* faecal pellets (Hunter 1977), are more abundant in the Shark Reef coarse-grained classes. The dominant 2ϕ modal class does not correspond with a greatly increased abundance of any particular grain type and is presumably due to hydraulic sorting.

Intra-reef sediment

Large areas of both Isaacs Reef (55%) and Shark Reef (37%) are made up of cemented internal sediment (Table 1). Cemented sediments from various parts of the reef all have very similar characteristics (text-fig. 9; Pl. 50, figs. 1, 3, 5; Pl. 52, figs. 4, 6). They are all subangular to very angular, fine to medium or medium-grained sands with a packstone texture. The dominant constituents being a brown micrite and spar cements (Pl. 52, fig. 6). Peloids are locally common (Pl. 52, fig. 4). Skeletal grains make up most of the remainder of these apparently grain-supported sediments. Foraminifers (mainly *Homotrema*) dominate (Pl. 52, fig. 6) and coralline fragments are the next most abundant. Traces of echinoid, bryozoan, serpulid, and spicule fragments also occur.

Discussion

In a simplistic view of patch reef sedimentation, a direct correlation might be expected between standing crops of carbonate secreting organisms and their abundance in inter- and intra-reef sediments. Scoffin *et al.* (1980) have investigated in detail the relationship between carbonate production and inter-reef sediments in a Barbados fringing reef. They find that sediments reflect most closely the primary frameworks of the reef. They also note that the sands are very well mixed in sediment patches across the Bellair reef. No carbonate production figures are available for Isaacs and Shark Reefs but a rough comparison can be made of abundance of grain types in inter-reef sediments with a visual impression of standing crops of producers. The only exception to this is the over-representation of *Halimeda* plates. This is well known from other regions (Garrett *et al.* 1970) and is accounted for by the rapid growth rate of this plant (Neumann and Land 1975). Evidence that bioerosion is a major source of sediment production from the reefs has been presented above. The removal of reef frameworks by sponges would be expected to result in a large proportion of coral and coralline algal grains in the silt size class of reef sediments. However, this size grade is not present as these sediments are continously wave washed and silts are probably carried out into deeper quiet waters. This was found to be the case in similar reefs by Moore and Shedd (1977). The increased abundance of primary framework grains in the 1 to 3ϕ classes in Shark Reef (corals and coralline algae) and Isaac Reef (corals) may be accounted for by bioerosion as both *Diadema* and parrot fish produce grains of this size (Schoffin *et al.* 1980). The higher energy conditions at Isaac Reef exclude these bioeroders from the coralline ridges which may explain the decrease in abundance of corallines in the 1 to 3ϕ classes at this location. Mechanical abrasion of coralline branches and crusts could account for the greater abundance in the coarser-size classes.

Intra-reef sediments are significantly different in both texture and composition from inter-reef sediments in both localities. The consistent finer grain size of the internal reef sediments (cf. Garrett *et al.* 1970) may partly reflect the exclusion of larger particles from entering internal cavities and partly the high intra-reef production of silt-sized sponge chips (Pl. 52, figs. 2–4). Grains which are well represented both within and outside the reefs are derived from organisms constructing or living on the reefs: coralline algae, molluscs, foraminifers, and echinoids, with the addition of *Millepora* in

Shark Reef. The remaining coral and *Halimeda* grains are only common in the inter-reef areas. The exclusion of *Halimeda* and coral fragments from the internal cavities may be explained by their occurrence in the lower sea floors around the reefs and suggests that waves do not carry these grains up into the reef interstices. However, with burial of the reefs they may be expected to be deposited above the internal sediments derived from the reefs.

The earlier investigation of coralline patch reefs by Ginsburg and Schroeder (1973) allows some comparisons. External reef sediments were not studied but internal reef sediments contrast with those from St. Croix reefs. The textures of the internal sediments of the Bermuda reefs varied from silt wackestones through to coarse grainstones. The sand-sized material appears to be largely derived from the reef framework and reef encrusters with grain abundance decreasing in the following order: crustose and branching corallines, *Homotrema*, molluscs and other foraminifers, *Halimeda*, echinoid, serpulid, and ostracod. This compares well with the internal sediment grains (all sizes) identified in the Cruzan reefs (text-fig. 9). However, the silt-sized debris was found to be quite different in the Bermudan reefs being composed of fragile and encrusting reef organisms mixed with planktonic organisms. This population was not seen in either of the reefs investigated here, in thin section or under S.E.M.

Comparisons of inter-reef sediments with other Caribbean examples (mainly coral reefs) show that they are texturally similar (Milliman 1967, 1969; Scoffin *et al.* 1980). These earlier studies have also found coarsely skewed (i.e. winnowed) coarse sands and gravels forming near-reef sediments. Compositionally it might be expected that the coralline algal reef sediments would differ from coral reef sediments. However, this is not the case (see Milliman 1973 for review). Other Caribbean reef sediments are dominated by either coral, coralline, and *Halimeda* grains and often show greater proportions of coralline grains than is found in the St. Croix coralline reef sediments. This apparent anomaly might be explained firstly by the abundance of coral stands around the Cruzan algal reefs (text-figs. 2, 3) and secondly by the fact that most of the erosion of the coralline framework is considered to be in the form of silt-sized sponge chips which are not deposited in the inter-reef sediments.

COMPARISONS AND CONCLUSIONS

Comparisons

Previous studies of shallow coralline reefs have been undertaken in the Caribbean (Boyd *et al.* 1963), the Mediterranean (Thornton *et al.* 1978), and Bermuda (Ginsburg and Schroeder 1973). Each study describes subcircular patch reefs (cup reefs), which may coalesce to form a lobate ridge. In vertical section, preferential growth of the corallines is visible on the outer edge which may result in a raised rim or crest and an overhanging lip. The upper surface of the patch reefs is generally dish-shaped, with less coralline growth and greater bioerosion in the central depressed area. With the exception of Ginsburg and Schroeder (1963) none of the previous authors have described the nature of the coralline reef framework. The corallines vary with location and sample sites on the reefs: Boyd *et al.* (1963) collected samples from the reef sides and reported *Neogoniolithon* (*Goniolithon*) *solubile*, *Archaeolithothamnium episporum*, *Lithothamnium sejunctum*, *Epilithon membranaceum*. Thornton *et al.* (1978) reported a framework of thin crusts of *N. notarisii* with some *Lithophyllum* indicating a similarity to the well-known Mediterranean 'trottoirs' (Pérès 1967; Laborel 1961). The most detailed study is by Ginsburg and Schroeder who describe frameworks of crustose corallines, *Millepora*, and vermetids. The Bermudan reefs are similar in many respects to those from St. Croix but differ in their greater height (8–12 m) and lower porosity. Coralline frameworks are constructed by laminar and columnar *Neogoniolithon* sp. with lesser *Mesophyllum syntrophicum*. They do not show the diversity of taxa or morphologies described in this paper. The complex sequences of reef growth, destruction, internal sedimentation, and cementation characteristic of patch reef formation (Schroeder and Zankl 1974; Scoffin and Garrett 1974) are common to the two examples.

Some similarities are also apparent with intertidal ledges built by crustose corallines in the Caribbean (Gessner 1970), on the Brazilian coast (Kempf and Laborel 1968), and in the

Mediterranean (Pèrès 1967; Laborel 1961). A comparison with the Pacific algal ridge systems (Emery *et al*. 1954) and deep-water coralline build-ups from the Mediterranean (Laborel 1961; Laubier 1966) is made in a recent review on coralline reef frameworks (Bosence 1983*b*).

Conclusions

1. The internal structure of two recent coralline reefs has been studied and nearly all the coralline algae living on the surface can be identified in thin sections from the reef interior. The occurrence of these preserved corallines can be used for palaeoenvironmental reconstruction.

2. Two main primary framebuilding coralline algae (*L. congestum* and *Porolithon pachydermum*) which today construct the intertidal algal ridge were abundant in the past in both reef sections.

3. Secondary reef frameworks occur in five associations of corallines (with *Homotrema* and vermetid gastropods) and each association is characteristic of different sub-environments on the reef and can thus be used in palaeoenvironmental reconstruction of the reef surface.

4. The occurrence of preserved primary and secondary frameworks in the slabbed reef sections permits a generalized reconstruction of past reef morphology and environment.

5. Isaacs Reef has alternated from a high- (*Porolithon* dominated) to mid-intertidal (*Lithophyllum* dominated) ridge during the last *c*. 2,200 years.

6. Shark Reef has had a more varied history alternating from an exposed intertidal reef to two periods of sheltered conditions during which a thick subtidal lip of secondary framework grew and the upper reef surface became reduced by bioerosion.

7. A predictable ecological succession of taxa and growth forms, and of subsidiary encrusters, is found in the primary frameworks.

8. Vertical sections through secondary frameworks illustrate predictable palaeoecological successions which equate well with previous settlement-plate experiments. Small fast-growing and presumed rapid dispersers are replaced by more massive, framework-building associations.

9. The major form of erosion on the reefs is bioerosion which is carried out mainly by clionid sponges and echinoids.

10. Inter-reef sediments are well- to poorly sorted coarse sands and gravels with symmetric to coarsely skewed distributions. Size ranges reflect the locally derived reef material and continual movement and winnowing by wave currents.

11. Compositionally, the inter-reef sediments reflect the composition of the reef frameworks, but are relatively depleted in coralline debris. Surprisingly, the sediments have a similar composition to Caribbean coral patch reefs. The relatively small amount of coralline material in the sediments is thought to be due to sponge erosion releasing silt-sized debris which is deposited in quieter waters away from the reefs.

12. Internal reef sediments are well-cemented and reflect the composition of the reef frameworks.

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